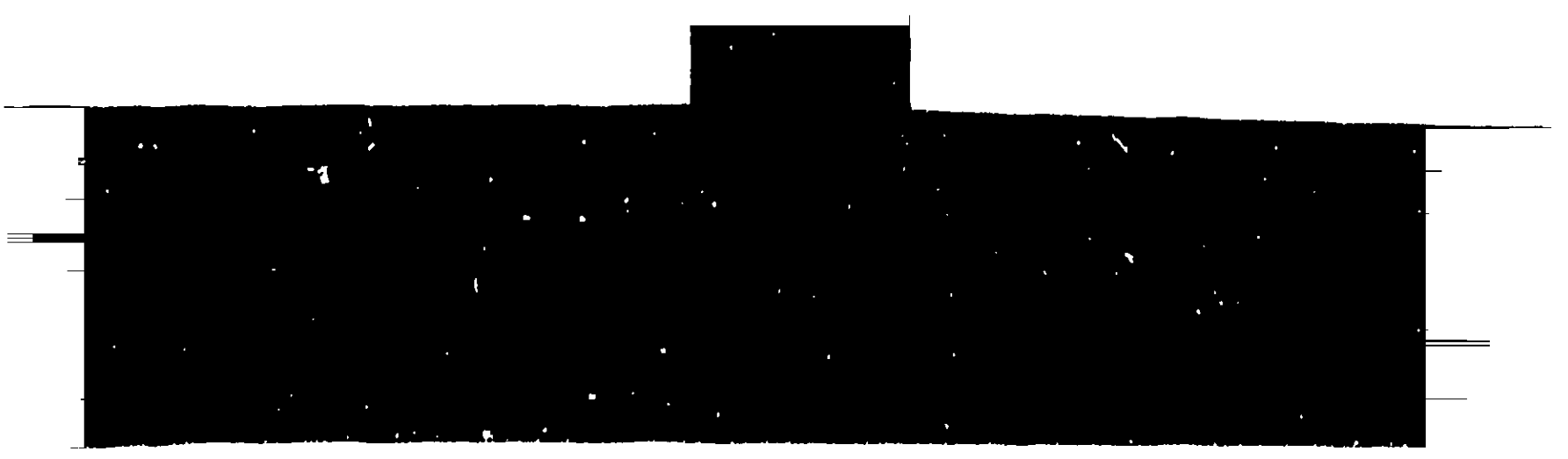

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# VOCAL BEHAVIOR OF ADULT CALIFORNIA QUAIL

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# VOCAL BEHAVIOR OF ADULT CALIFORNIA QUAIL

H. Warrington Williams

This paper describes the calls of adult California Quail (*Lophortyx californicus*) in terms of their form, causation, and function. A later paper will report on the derivation of adult calls from the repertoire of the chick.

Previous studies of this species, concerned with life history, habitat, food habits, and social behavior, placed little emphasis on vocal communication (Emlen and Lorenz, 1942; Howard and Emlen, 1942; Genelly, 1955; Raitt, 1960). Sumner (1935) provides the most complete listing of calls and the contexts in which they are given.

## Methods

This study lasted from June 1961 through August 1964. It was made with captive quail except for a few free-living individuals in Salt Lake and Cache Counties, Utah.

The adult quail were kept in four outdoor pens (12,000 square feet total) with wire tops and sides. Natural and transplanted vegetation provided nesting and escape cover. In late winter two of the larger pens were partitioned to form smaller pens for nesting pairs, groups of females, and groups of males. Canvas screens visually separated males and females in the pens housing only one sex. Wheat or commercial laying feed and water were provided.

Prior to each breeding season 10 to 15 adults of each sex were visually isolated in individual cages. These birds were used in experimental situations as described below. All the quail were individually marked. Between 50 and 100 adults were kept throughout the entire study. All came from one of three sources: wild birds trapped in Salt Lake and Utah Counties, Utah; game bird breeders in Utah and California; and progeny from the above stock.

Recordings were made with a Model T1500 Wollensak or Model 730 Voice of Music recorder at tape speeds of 7½ or 3¾ inches per second. The microphone (Electro-Voice 664) was usually within 15 feet of the calling bird. The recordings were played back with the same recorder to transfer them to the audiospectrograph (Kay Electric Company Sonograph Model 661A). All audiospectrographs were made with the FI-1 circuit and a "wide band" filter setting. The india ink tracings of audiospectrographs used in the figures were selected as representative by comparing sonograms of the same call from at least five birds.

I watched the birds from darkened rooms adjoining the pens or from behind canvas blinds hung on the wire outside the pen. Observations covered the entire annual cycle with emphasis on the breeding period; most were made in the morning and evening to avoid the inactive noon period characteristic of most galliforms.

Robert L. Rumsey, to whose work I often refer below, was studying the nonvocal behavior of this species in the same place at the time of this study.

## Results

The following brief outline of the life history of the California Quail is presented to help understand the vocal behavior.

California Quail are gregarious through a large part of the year. In mid- to late summer neighboring family groups, pairs without young, and unmated birds—primarily males—move together to establish winter coveys (Sumner, 1935; Raitt and Genelly, 1964). The resultant groups are remarkably sedentary during the winter, often occupying areas less than 0.5 mile in diameter (Howard and Emlen, 1942; Raitt and Genelly, 1964). Covey ranges overlap in areas of high density, and under such conditions groups split and recombine repeatedly throughout the season (Sumner, 1935), although Howard and Emlen (1942) show that "social barriers of non-recognition discourage inter-covey mixing." Aggression between coveys has also been described for the Bobwhite Quail (*Colinus virginianus*) (Errington, 1933) and the Chukar Partridge (*Alectoris chukar*) (Williams and Stokes, 1965). Individual members of a penned group are rarely intolerant in winter. Birds often cluster during extremely cold weather, roosting in body contact under brush and in trees. Main requirements during this period of the year are adequate food and shelter.

Covey disintegration following onset of social intolerance begins in late February in some regions, but courtship activity and pair formation more often occur in March and April (Sumner, 1935). Covey breakup is normally complete by late May and considerable, often long distance, movement occurs during this period (Raitt, 1960). Pair formation within the covey results in many sedentary pairs that nest in the general area occupied by the covey during the winter. Some unpaired birds, particularly males, may cover relatively long distances in seeking a mate. Genelly (1955) and Emlen (1940) show that unmated birds are of two types, nomadic and sedentary. Sedentary males may be spaced somewhat territorially at distances ranging from 20 feet upward, with highest densities occurring in areas favored by nesting pairs. The dominant territory-holding individuals tend to be adults, while nomadic, unmated birds are usually yearlings and subdominant adults (Genelly, 1955).

Pair formation is essentially complete by early June. Nesting follows with peak of hatching in late June or July. The female normally incubates, but I twice saw penned males incubating after the female died. The male remains in the vicinity of the brooding female and helps in brooding and care of chicks. Although precocial, the young need brooding and are extremely susceptible to chilling for the first four weeks. Koskimies (1962) found that *Lophortyx* chicks at hatching produce only 20 per cent of the body heat necessary to maintain homeostasis.

The adult California Quail has at least 14 calls. I have divided these into four categories modified from Collias (1960): social contact, alarm, reproductive including agonistic and sexual, and parental. The causation and function of several calls vary with season and social context and are

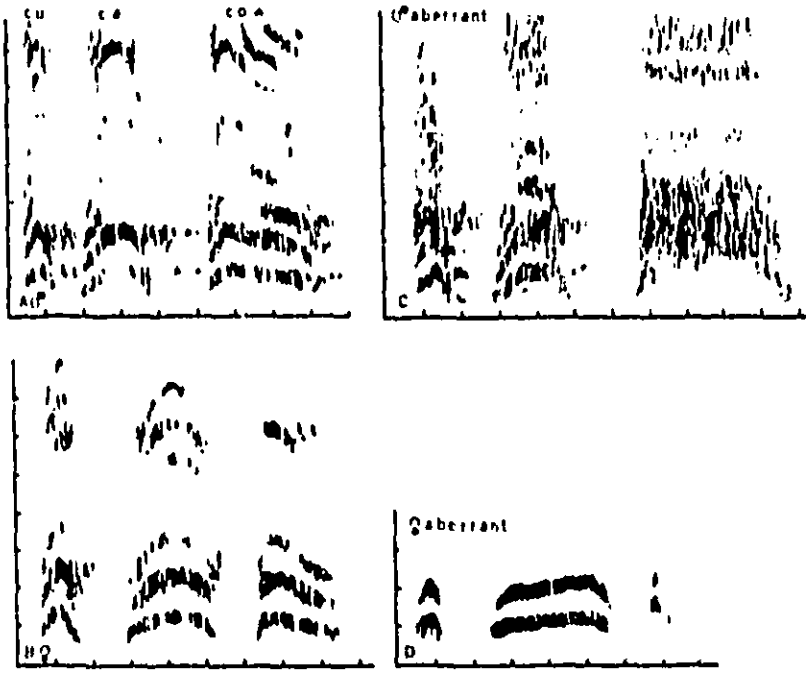


FIGURE 1. *Cu ca cow* call of the California Quail. Intervals on horizontal axis are 0.1 second; the vertical axis is frequency intervals of 1.0 kc/sec.

described under separate categories. I initially named each call by orthographic description to avoid implications of function. Sumner's (1935) terms follow in parentheses.

TABLE 1

COMPARISON OF MALE AND FEMALE *CU CA COW* CALLS

| | Time (sec) | | | | Mean frequency (to nearest 125 cycle/sec) | | |
|---|---|---|---|---|---|---|---|
| | Total length of call | *cu* to *ca* | *cu* to *cow* | *ca* to *cow* | *cu* | *ca* | *cow* |
| Females (10) | | | | | | | |
| *Minimum* | 0.55 | 0.16 | 0.39 | 0.10 | 1,750 | 1,750 | 1,500 |
| Maximum | 0.98 | 0.30 | 0.61 | 0.46 | 2,625 | 2,375 | 2,375 |
| Mean | 0.72 | 0.20 | 0.51 | 0.31 | 2,012 | 2,250 | 2,150 |
| SD | 0.11 | 0.04 | 0.06 | 0.07 | 714 | 661 | 863 |
| Males (10) | | | | | | | |
| Minimum | 0.62 | 0.15 | 0.43 | 0.17 | 1,750 | 1,875 | 1,625 |
| Maximum | 0.79 | 0.40 | 0.57 | 0.39 | 2,500 | 2,125 | 1,900 |
| Mean | 0.74 | 0.24 | 0.53 | 0.30 | 2,175 | 2,213 | 2,175 |
| SD | 0.06 | 0.06 | 0.04 | 0.06 | 740 | 1,076 | 1,161 |

TABLE 2
Variation of *cu ca cow* Calls for Two Males[1]

| Date recorded | Total length of call | Time (sec) | | | Mean frequency | | |
|---|---|---|---|---|---|---|---|
| | | *cu* to *ca* | *cu* to *cow* | *ca* to *cow* | *cu* | *ca* | *cow* |
| | | | Male 1 | | | | |
| 23 Feb. '64 | 0.69 | 0.25 | 0.50 | 0.26 | 2,475 | 2,250 | 2,125 |
| " | 0.68 | 0.26 | 0.50 | 0.24 | 2,875 | 2,750 | 2,750 |
| " | 0.69 | 0.22 | 0.46 | 0.27 | 2,375 | 2,250 | 2,250 |
| " | 0.66 | 0.24 | 0.47 | 0.27 | 2,375 | 2,475 | 2,375 |
| " | 0.67 | 0.24 | 0.50 | 0.25 | 2,375 | 2,250 | 2,250 |
| Mean | 0.68 | 0.24 | 0.49 | 0.26 | 2,471 | 2,373 | 2,350 |
| 24 Feb. '64 | 0.80 | 0.30 | 0.57 | 0.29 | 2,500 | 2,500 | 2,500 |
| " | 0.72 | 0.27 | 0.53 | 0.26 | 2,375 | 2,250 | 2,250 |
| " | 0.82 | 0.26 | 0.57 | 0.29 | 2,500 | 2,375 | 2,500 |
| " | 0.78 | 0.39 | 0.56 | 0.27 | 2,375 | 2,250 | 2,375 |
| " | 0.78 | 0.26 | 0.59 | 0.25 | 2,750 | 2,625 | 2,625 |
| Mean | 0.78 | 0.29 | 0.56 | 0.27 | 2,500 | 2,400 | 2,450 |
| | | | Male 2 | | | | |
| 23 Feb. '64 | 0.69 | 0.21 | 0.51 | 0.30 | 2,250 | 2,250 | 2,125 |
| " | 0.69 | 0.24 | 0.51 | 0.27 | 2,500 | 2,375 | 2,375 |
| " | 0.73 | 0.21 | 0.51 | 0.31 | 2,125 | 2,125 | 2,125 |
| " | 0.72 | 0.24 | 0.55 | 0.31 | 2,250 | 2,250 | 2,250 |
| " | 0.68 | 0.22 | 0.50 | 0.29 | 2,625 | 2,625 | 2,500 |
| Mean | 0.70 | 0.22 | 0.52 | 0.30 | 2,450 | 2,535 | 2,235 |
| 24 Feb. '64 | 0.69 | 0.21 | 0.54 | 0.37 | 2,250 | 2,250 | 2,250 |
| " | 0.73 | 0.26 | 0.56 | 0.31 | 2,475 | 2,375 | 2,375 |
| " | 0.76 | 0.25 | 0.52 | 0.27 | 2,500 | 2,500 | 2,500 |
| " | 0.74 | 0.25 | 0.56 | 0.30 | 2,375 | 2,375 | 2,375 |
| " | 0.76 | 0.25 | 0.60 | 0.35 | 2,000 | 2,125 | 2,125 |
| Mean | 0.73 | 0.25 | 0.56 | 0.32 | 2,300 | 2,325 | 2,325 |

[1] Calls recorded during 1-hour period following playback of female *cu ca cow* calls.

## Aggregation and Contact Calls

*The cu ca cow (assembly) call.*—This loudest and most frequently heard call is given by both sexes throughout the year (Figure 1). The call is repeated from one to nine times. Additional *cu ca* syllables often precede or are interspersed between discrete *cu ca cows*. The term *cu ca cow* in the following discussion refers to one or more *cu ca cow* syllable groups given in series. Variation existed between and within individuals of both sexes (Tables 1 and 2).

The quail normally stand while calling but occasionally move about. In both cases the head is elevated slightly and the bill opens on each syllable. The call is normally loud, but birds interrupted in their calling often continue softly for a brief period. The *cow* syllable is at times omitted here or when the individual has just begun to call.

Nonbreeding quail in the wild give the call after the covey has dispersed. Imitation of the call by mechanical means may stimulate members of a nondisturbed covey to call (Sumner, 1935). The call was most frequent


Figure 2. (A) and (B) variations in the *ut ut*; (C) *ut ut* grades to *cu ca* note, and (D) *tu tu* calls of the California Quail. Scale as in Figure 1.

in the pens when one bird of either sex was separated from the group. Calling by this separated bird elicited calling by one or more members of the covey. Playback of recorded *cu ca* notes could also elicit calling by penned birds. Calling in the nonsexual covey situation ceases when the separated individual regains visual contact with the group. The call is also given in sexual and parental situations having a similar causation (i.e. one individual separated from group or mate (see below)

*The* ut ut *call* (*conversational notes*).—The *ut ut* is a low frequency, repetitive call given throughout the year (Figure 2A and 2B). It is similar for all individuals and both sexes. It occurs most often as a series of notes sometimes continuing for a minute or more. Birds call while moving or loafing close to others. The bill is sometimes slightly open during calling, but at other times no bill movement is perceptible. The tail flicks slightly with each note. Members of a covey separated visually by a cloth barrier paced opposite one another on either side of the screen while giving the call.

Adults confined in adjacent individual cages and not in visual contact gave the call during active periods or after a disturbance. Birds that had been separated from a group or mate called *ut ut* loudly immediately following separation. The note is given at 0.2-second intervals in a con-

tinuous series. This grades to the *ca ca* notes and finally to the complete *ca ca cow* sequence (Figure 2C). The *ut* note and the *ca* note of the *ca ca cow* call are similar in configuration (Figures 1 and 2).

Adults give a similar call sounding more like a *mo mo mo* to their chicks. The *ut ut* grades to the food call with the discovery of new food or movement of the group to the food hopper.

*The* tu tu *food call* (*conversational notes*).—Many galliforms, including the Bobwhite Quail (Williams et al., 1968) and Chukar Partridge (Stokes, 1961), utter a food call while in a covey. In California Quail the call is a low, repetitive *tu tu* given by both sexes (Figure 2D). Males call more frequently than females. I stimulated the food call by depriving birds of food for a day or by introducing food, such as meal worms (*Tenebrio*) or mixed grains, not normally seen by the quail. The bird first discovering the food gave the call intermittently as it began feeding. Others on hearing the call moved to the calling individual and fed. They gave the food call more consistently to grain in small piles than to grain scattered on the pen floor. Quail gave the call immediately on finding the food. Calling continued for a brief period as the bird began to feed, but waned as feeding continued. Other birds sometimes called as they approached and fed. Playbacks of the quail's food call through a hidden ground-level speaker caused birds to approach. Food calling in sexual situations, termed tidbitting (Domm, 1927), is discussed in a later section.

### Alarm Calls

The alarm notes of the California Quail are associated with the presence of aerial and ground predators, freezing following alarm, running away, and severe distress.

*The* pit pit *call* (*alarm note*).—Next to the *ca ca cow*, the *pit pit* call, a series of metallic-sounding *pits* (Figure 3A), is the most frequent call of the California Quail. Both male and female birds give the call at all seasons of the year with little variation among individuals or sexes.

The most common releaser of the call was a cat, dog, or rat in or around the pens. One bird seeing a potential predator on the ground called; others then became alert and began to call. The response of a group of quail on hearing the call is to form a loose, alert aggregation. On occasion the group moved toward a cat outside the pen in a mobbing-type behavior. Birds calling are very erect and the bill opens slightly on each note. The frequency with which the syllable is repeated depends on the strength of the stimulus eliciting the call. When a dog was placed in a small pen with a group of quail, the calling rate increased (Figure 3B).

Strange objects placed in the pen with the quail also elicited this call. When I presented a stuffed toy dog to birds, the invariable response was

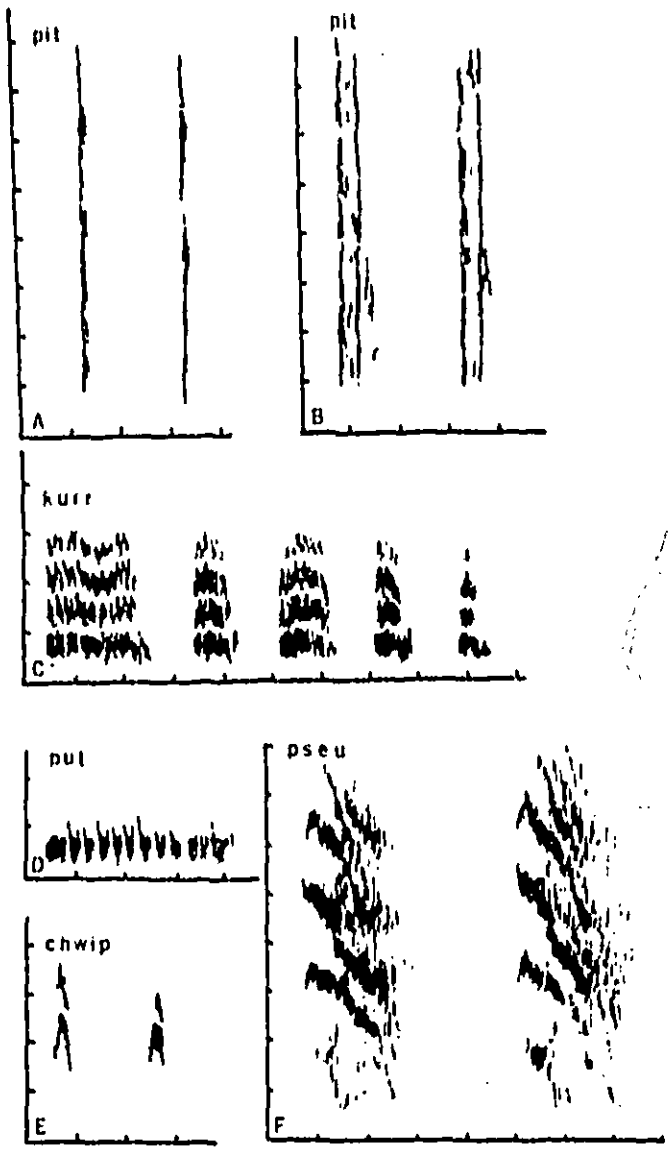


Figure 3. The alarm calls of the California Quail. Scale as in Figure 1.

*pit pit* calling. Moving familiar objects such as a pile of rocks to a new location in the pen produced the call on occasion. Habituation in these instances was rapid and the call soon stopped.

Birds also call *pit pit* in nonspecific situations in which they appear uneasy or nervous. Individuals separated from a group or mate intersperse the call with the *cu ca coe*. Pairs with chicks and chicks themselves also call in similar situations.

*The* kurr *call (signifying extreme fright).*—Birds seeing Sparrow Hawks (*Falco sparverius*), California Gulls (*Larus californicus*), or other large birds flying over the pens gave a low, throaty *kurr kurr kurr* (Figure 3C). Males, who are normally more alert, give the call more frequently than females. The caller crouches or darts to nearby cover after calling. Other birds hearing the call crouch or freeze if in sufficient cover or run to cover if in the open. Newly trapped wild quail are more prone to give this call than birds confined for longer periods. Sparrows alighting on top of the pens elicited the call in these wild birds. The response here was apparently to the sudden appearance of the stimulus rather than to the actual silhouette presented. Attempts to stimulate the call with a hawk silhouette were largely unsuccessful after the first few presentations of the model.

The aerial alarm call is essentially a response to a strange object above the ground. My movement in the observation window 5 feet above the pen floor at times elicited this call. Again newly penned individuals reacted initially but soon habituated. Sumner (1935: 204), although he does not designate the call as one of aerial alarm, comments that "when the field worker hears this call in the Santa Cruz Mountains he will be correct about 75 per cent of the time in concluding that a Cooper (*Accipiter cooperii*) or Sharp-shinned Hawk (*Accipiter striatus*) is after the birds." This note frequently precedes the *put put* (Figure 3D) call and the *chwip chwip* note.

*The* put put *call.*—This low note sounds much like a distant outboard motor. The call is most frequently given following a period of aerial disturbance. Once when I startled a group of newly acquired individuals, a male gave the aerial alarm call and the group disappeared under brush. I could see only the male who had originally called and two females. All birds crouched silently for 3 minutes. When one female finally moved, the male who was watching me gave this call. The female again crouched. Movement at the window again stimulated the call from this male. I feel that this call serves to prolong crouching by a group following disturbance from the air. One bird still in visual contact with a potential predator gives the call, and the group responds by remaining crouched and hidden.

*The* chwip chwip *call.*—The soft *chwip chwip* note (Figure 3E) is given by both sexes as they flee on foot from a large predator such as a man or dog. I heard the call most frequently when netting birds. The harder an individual is pressed, the more frequently it calls. The call is always

associated with alarm situations that produce a running, avoidance behavior. Subordinate birds pursued by a dominant do not give the call. I term the call one of running alarm. It apparently carries little if any signal value, as playbacks of the call to undisturbed birds produced no visible response. It may represent low intensity distress comparable to the following vocalization.

*The* pseu pseu *call* (*the distress cry*).—Both sexes held in the hand give frequent and loud *pseu pseu* calls (Figure 3F). Sumner (1935) comments that a bird seized or about to be seized by a Cooper's Hawk gives the same call. It is comparable to the call many galliforms give when held in the hand. The response was variable; some birds called immediately on being seized, others remained quiet even when held by a foot or wing. Females and young birds of both sexes can be induced to call more frequently than adult males. Genelly (1955) reported birds giving the *pseu* call and approaching a bird calling in distress. He suggests that this call functions as a releaser of a type of mobbing behavior useful in the distraction of enemies.

The call shows marked variation between individuals, but its configuration is basically the same with both sexes and all individuals. *Pseu pseu* calls elicit both *pit pit* alarm calls and the *cu ca cow* from nearby individuals. This is particularly true of juvenile *pseu* notes.

### Agonistic and Sexual Calls

Many calls of the California Quail occur solely during the breeding season. These are sexual or agonistic depending upon the behavioral context in which they are given. The previously described *cu ca cow* call and the food call, although given during the nonbreeding season, assume a sexual function during the breeding season. They are treated in this context now.

*The sexual* cu ca cow.—The *cu ca cow* is seldom heard in winter unless individuals are separated from a group. With the approach of spring, the frequency of *cu ca cow* calling in both sexes increases even when not separated. I first heard the call between 8 and 15 February in 2 of the 3 years of the study, and by 1 March in the 3rd year. Increase in calling coincides with covey breakup (Sumner, 1935). To test the influence of increasing photoperiod and subsequent change in sexual activity on calling rate, I placed three males and three females, caged as two pairs, a lone male, and a lone female, under a 16-hour photoperiod indoors during January. Recorded *cu ca cow* calls of both sexes were then played to these individuals at 3-day intervals. Of the 250 calls elicited by this playback, 92 per cent came from the two unpaired individuals (Table 3). The lone male, upon hearing the recorded call of the female, not only called

TABLE 3
Change in *cu ca cow* Calling in Response to Recorded *cu ca cow* Playbacks[1]

| Days under lights | Mean calling per 5 min | |
|---|---|---|
| | Male playback | Female playback |
| 1-11 | 4 | 2 |
| 12-31[2] | 11 | 10 |

[1] 10 trials completed in January 1964.
[2] First sexual behavior seen after 12 days of lighting, first egg laid on 29th day.

in reply but also made strong attempts to fly out of the cage. The sharp increase in calling by both sexes corresponded with the appearance of sexual behavior in the paired individuals. I found *cu ca cow* calling increased in the period (spring) for which Lewin (1963) demonstrates an increased gonadal activity.

Although the sonograms do not indicate a great difference between sexes (Table 1), the mean number of *cu ca cow* syllables repeated in a series without interruption is 5.9 for males and 2.6 for females (Figure 4). This difference was not apparent during the nonbreeding period when both male and female repeated the *cu ca cow* an average of 2.8 times in a series. This suggests that sex recognition in this call is related to the total length of calling for any given sequence. Playbacks of female calls (a *cu ca cow* repeated three times) produced a stronger calling response in five individually caged males than did the call of a male (a *cu ca cow* repeated six times) (Table 4). Playback of only half a male call did not elicit a

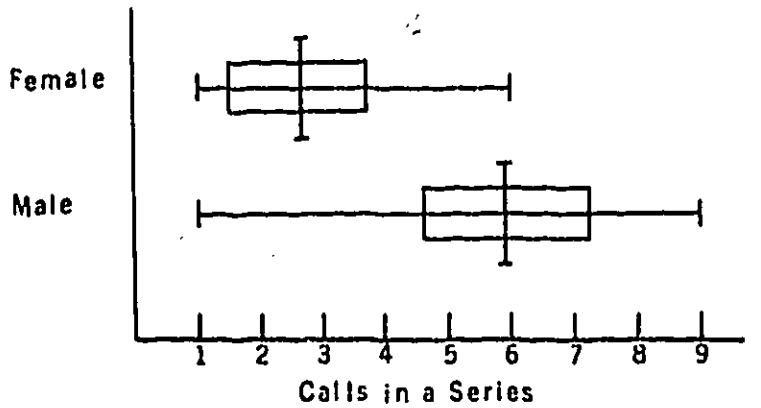


Figure 4. Numbers of *cu ca cow* notes repeated in a series by male and female quail. The vertical lines represent the means. Horizontal bars represent standard deviation around the mean. N for both sexes is 250 series of calls.

TABLE 4
MALE AND FEMALE RESPONSE TO RECORDED *CU CA COW* PLAYBACKS[1]

| Sex of responding bird | Mean *cu ca cow* calls per 5 min in response to playback | |
|---|---|---|
| | Playback of male's call | Playback of female's call |
| Male | 0.7 | 5 |
| Female | 0.5 | 0.9 |

[1] Calls from 5 individually caged male and female quail during 15 trials for each sex in March.

calling response, suggesting that other information than length of the call is necessary to distinguish the sex of the caller.

Unmated females give the *cu ca cow* during the first half of the breeding season. Unmated males call early in the season but by April begin the *cow* call, considered in the following section, with concurrent reduction of *cu ca cow* calling.

To determine the relationship between male social rank and *cu ca cow* calling, I played recorded male and female *cu ca cow* calls to five individually caged males during March 1964. Calling response was tabulated for the following 5 minutes. This procedure was repeated for 15 days. Only five male *cu ca cow* calls responded to male playbacks, but female playbacks produced 70 responses. Social rank of each male was later determined by outcome of paired encounters. The fourth-ranking bird called 38 times, the two top-ranking birds gave 13 and 10 calls respectively, the third-ranking bird called 4 times, and the fifth-ranking once. These males were individually caged during the tests and dominant birds could not inhibit calling by the subordinates. Had they been together, calling rates might have been more closely correlated with social rank. This compares to *rally calling in the Chukar Partridge* where the top-ranking individuals gave 90 per cent of the calls (Williams and Stokes, 1965). The rate of *cu ca cow* calling in this situation may represent a level of sexual rather than aggressive motivation as implied in social rank.

To see if the female *cu ca cow* call would attract an unmated, sexually active male, I placed an unmated male in a 3 × 12-foot wire pen with speakers located at each end and allowed it to adjust to the conditions for 15 minutes. Then the call of a female was played alternately through the right and left speaker. The recorded call elicited not only calling by the male, but also orientation, movement, and courtship to the sound source (Table 5). Marler (1956) shows that the unmated male Chaffinch (*Fringilla coelebs*) makes courtship postures on hearing the call of the female looking for a mate without actually seeing her.

TABLE 5
Male Response to Female *cu ca cow* Playbacks[1]

| Playback to (no. trials) | No. times orients to | | No. times moves to | | Calls | Courtship displays | |
|---|---|---|---|---|---|---|---|
| | Left | Right | Left | Right | *cu ca cow* | Tidbits | Back roll |
| Left (21) | 10 | – | 10 | – | 4 | 3 | 0 |
| Right (21) | – | 12 | – | 9 | 4 | 5 | 1 |

[1] Response of three males to call of female played through speakers at opposite ends of narrow pen.

Females tested in the above situation called in response to the male *cu ca cow* but did not move toward the sound source. The change in the male's orientation and subsequent movement to the source of the female's call tends to support Sumner's (1935) conclusion that the male seeks out the unmated female more than the reverse.

*Cu ca cow* calling dropped sharply following pair formation. Paired birds seldom called unless separated. Table 6 shows calling by both sexes during a 15-minute period following removal of one member of a pair. During May and early June 1963 the female was removed from the male and placed in a small holding cage out of his sight 50 to 100 feet away. The procedure was repeated during the same period in 1964 with the male removed from the female. The reduced calling by the bird placed in the cage was apparently a result of handling, as the undisturbed bird in the home pen called first in 15 out of the 16 trials. Mean time to first call following separation was 5.2 minutes. Mean time between first call of one bird to first call and answering by the second bird was 25 seconds. The short time interval between the first call and the answering call suggested that pair members are able to recognize their mate's call.

To examine this possibility I separated members of two pairs (both visually and acoustically) and to each played prerecorded calls of its mate intermixed with calls of two other birds of the same sex. Each bird called only in answer to its mate's call. Both sexes called within 10–15 seconds after the mate's call. This test did not preclude the possibility that separated birds would with time answer the calls of birds other than their mates. In three instances the female was removed from the mate and prevented from answering his *cu ca cow* call. The male called *cu ca cow* for 30 minutes to 1 hour and then began to *cow* call. Thus a bird given a choice answers only the call of the mate. If the mate does not call, the bird again responds as an unmated individual. Kozlowa (1947) reports a similar instance of mate recognition by call for the Ring-necked Pheasant (*Phasianus colchicus*).

Marler (1960: 362) has postulated that a call's species-specific prop-

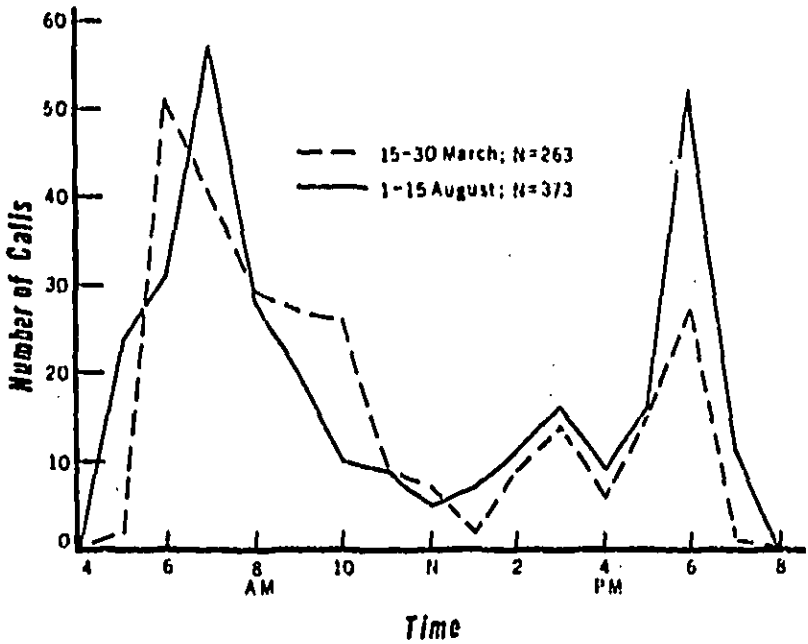


Figure 5. Total *cu ca cow* calls given by a male during a 15-day period in March and August 1964.

erties, song in particular, may lie in its overall time pattern, while individuality is possible by detailed changes of pitch. Thus the call conforms to that typical of the species while conveying information identifying the individual. The sonograms of *cu ca cow* calls from various individuals show a pattern consistent with this (Table 1 and Figure 1). Individuality may be conveyed by discrete patterns of overtones and detailed frequency variations of the main tone within rather fixed limits.

The female *cu ca cow* call is a strong stimulus eliciting approach by the male. In the summer of 1964 the male of a mated pair (the female had laid four eggs) escaped from a pen at my home. The female gave the *cu ca cow* immediately following the male's escape. He responded with the same call from a distance of 100 yards. I removed the female from the pen and played her recorded *cu ca cow* call through a speaker inside an empty trap. Her mate approached on foot to a hedge bordering the lawn. He called several times from this cover and seemed hesitant to cross the open ground around the house. I played the female's call at intervals during a 20-minute period and the male made a calling response each time. He finally ran across the lawn and entered the trap.

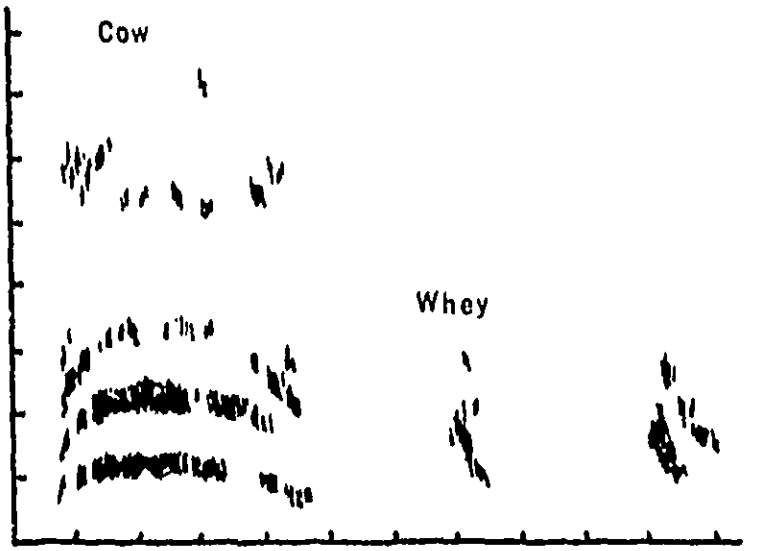


*Figure 6. The cow-whey calls of the California Quail. Scale as in Figure 1.*

*Diurnal pattern of* cu ca cow *calling.*—In the early spring and fall *cu ca cow* calling occurs most frequently during early morning and late evening as illustrated in Figure 5. Genelly (1955) heard the least amount of calling in wild quail from mid-June to mid-August. Increased calling coincides with increase in sexual activity in spring and recrudescence in fall. The male of Figure 5 began *cow* calling, with reduction of *cu ca cow* calling, in late April. The shape of the calling curve shown here is typical of several galliform and passerine birds (Williams and Stokes, 1965). Inclement weather in the morning delays the onset of calling. My impression was that quail were inactive for a period after waking and no calling occurred until general activity began.

*The* cow *call (single cow of the breeding season).*—The *cow* note is given only by males during the early portion of the breeding season. It is similar to the last syllable of the *cu ca cow* call, but longer (Figure 6A). Males call most frequently from an elevated position. The male stands erect, elevates his head, and opens his bill as he gives each note. A faint call sounding like *whey whey* follows each *cow* call but is inaudible at more than 30 feet (Figure 6). Only males housed away from females gave the call, and then only from April to June and August to September. This corresponds to the period of maximum testicular size Lewin (1963) describes.

TABLE 6

MALE AND FEMALE *CO' CA COW'* CALLING FOLLOWING SEPARATION[1]

| Trial | Male removed from female (March 15-June 5 1963) | | Female removed from male (May 15-June 5 1964) | |
|---|---|---|---|---|
| | Male calls | Female calls | Male calls | Female calls |
| 1 | 0 | 0 | 35 | 0 |
| 2 | 1 | 22 | 20 | 0 |
| 3 | 0 | 24 | 20 | 0 |
| 4 | 0 | 12 | 48 | 11 |
| 5 | 0 | 40 | 18 | 30 |
| 6 | 5 | 1 | 14 | 2 |
| 7 | 5 | 18 | 6 | 6 |
| 8 | 20 | 43 | 20 | 3 |
| Total | 40 | 169 | 178 | 85 |
| Mean | 5 | 21 | 22 | 11 |

[1] Calls given during 15 minutes following separation of pair.

*Cow* calling was most frequent during the early morning and late evening. Calling rates varied from 1 to 10 calls per minute. One male called at a rate of 8.6 calls per minute over a 15-minute period. Sumner (1935) recorded as many as 7 calls per minute with an average of 3.

In a pen containing five males, the dominant bird called *cow* frequently from a rock pile at the back of the pen. The four subordinate birds remained in the front of the pen but did not call. When a female was introduced into the pen she was immediately courted by the three top-ranking birds until the alpha male repelled the other two. In three of five situations of this type the second-ranking male went to a rock pile and called *cow* as the dominant bird courted the female. The alpha male interrupted courtship on each occasion to attack the calling bird.

The *cow* note was heard most often in April and May. To test the influence of the male gonadal hormone in *cow* calling, I gave five males and five females testosterone proprionate daily in 1 mg doses during July 1964. The sexes were kept in separate pens. The two top-ranking males began to give the *cow* call after 10 days of injection. The number of *cow* calls varied from 1 to 7 per minute with a mean of 4. Fighting occurred on the 5th day of hormone administration. Females were not aggressive and did not *cow* call.

Sumner (1935) states that unmated males call *cow* on acquiring a territory. The dominant's attack on birds calling from the rear of the pen may represent defense of an area, the attack having been elicited by their *cow* call. Injection of testosterone late in the summer after breeding produced aggressiveness and *cow* calling. Hence the call may be like song in passerines—it functions both to attract a mate and to repel rival males.

*The sneeze call (squill of defiance).*—The loud notes of the sneeze call

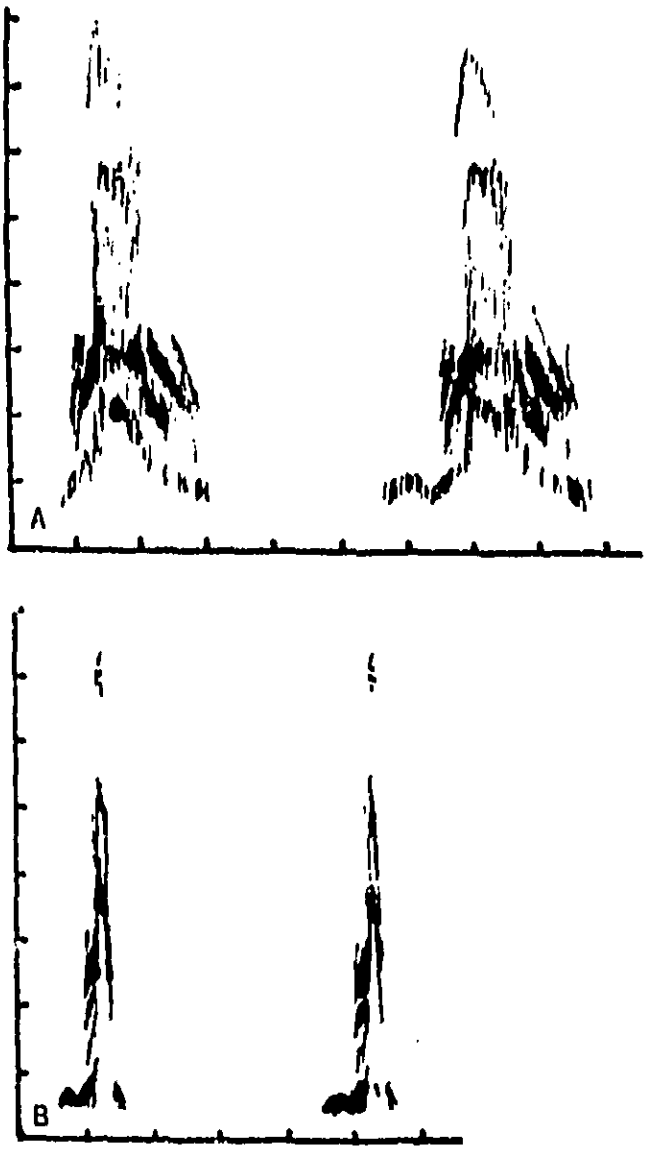


Figure 7. (A) sneeze and (B) *wip wip* calls of the California Quail. Scale as in Figure 1.

are given almost solely by the male and only during the breeding period. Only one female gave the call during the 3 years of the study. The call is a series of short, vehement sneezes given in rapid succession (Figure 7A). The male on calling opens his beak and throws his head back rapidly so that the beak is almost vertical. The movement exposes the male's conspicuous black throat patch. The call is most frequent during aggressive encounters between males before they establish a clear dominance relation. Aggressive males that are confined in the presence of their mate and an additional male, but which cannot reach either bird, give the call frequently. A male confronted with his own image in a mirror also called frequently between attacks on the image. Results from 20 paired encounters between two unmated males in the presence of a female showed that the dominant bird gave a total of 14 series of sneeze calls, the subordinate only 4. Calling by the subordinate bird always occurred only before a final dominance relation was established.

*Alternation of female* cu ca cow *and male sneeze calls.*—During the breeding season unmated males announced their presence and unmated status by means of the *cow* call, but females conveyed their unmated status and location with the *cu ca cow* call. After pair formation neither sex used either of these calls unless separated; both then gave the *cu ca cow* call (Table 6). During the previously described tests separated males sometimes superimposed the sneeze call over the first four or five, if not all, of the *cu ca cows* given by the female mate. The antiphonal relationship of these two calls has been considered elsewhere (Stokes and Williams, 1968).

This situation is unusual in that a call produced by one bird but received by two birds in different social situations, the male mate versus an unmated male, can produce two different responses. The *cu ca cow* by the separated female apprises the mate of her location, but also announces to any unmated males the presence of an apparently unmated female. The mate's aggressive sneeze call serves to repel the potentially rival male.

*The* wip wip *call* (wip wip *of the male*).—During the breeding season aggression between males is always accompanied by the *wip wip* call (Figure 7B). The call is given rapidly and repeated intermittently during aggression. The calling male stands erect and opens his bill as each note is given. The call is inaudible beyond 60–75 feet. In encounters between males the call was most frequently associated with dominance (Table 7). The two top-ranking males gave 85 per cent of the 294 series of calls recorded.

*Wip wip* notes are also given to strange and mated females. A female introduced into an all-male pen was chased by the dominant males, and *wip wip* notes were common during chasing. This note is also given during

TABLE 7
Relation of *wip wip* Calling to Social Rank[1]

| Social rank | Calls | |
|---|---|---|
| | Number | Per cent |
| 1 | 172 | 58 |
| 2 | 80 | 27 |
| 3 | 28 | 10 |
| 4 | 14 | 5 |
| 5 | 0 | 0 |

[1] Five males during April–June 1964.

copulation (see copulation calls). Males approach the female from the rear and begin the call as they mount. On several occasions the male called after he had grasped the female by the base of the topknot.

To determine the motivation of the *wip wip* call the following tests were performed. I visually isolated five male and five female quail in April 1964. In May and June pairings were made between male and female, female and female, and female with two males. Placing a female with two males was an excellent way to elicit aggression when initial pairings between males did not provide decisive dominant-subordinate relations. The quail were released together into an outside pen (40 feet square and screened from adjoining pens) and watched for 15 minutes.

Females were rarely aggressive to each other. Instead they frequently dust bathed—often side by side in the same dust bowl—preened, fed, and paced. Most common calls were the *ut ut* and *cu ca caw*. Birds oriented during calling to birds in adjacent pens. No definite social ranking was apparent among females.

In male-female encounters both birds paced the area briefly after introduction. Males stood erect and frequently gave *pit pit* calls intermixed with *wip wip* notes. Initially dusting and preening were common. This was always true of birds kept on wire. Male courtship consisted largely of tidbitting with and without the food call. A backroll display in which the back was inclined to the female, tail wagging, and feather-ruffle-shake (feathers ruffled followed by shaking) also occurred during courtship. Successful copulations occurred in 21 of 25 male-female pairings. The stimulus provided by a female crouched while dusting regularly produced a copulation attempt by the male. Females also stimulated copulation by crouching as they uttered the copulation call.

Aggressive and sexual behavior occurred in two male-one female encounters. Both males attempted to court the female immediately following introduction. Fighting ensued and a dominant-subordinate ranking was established, normally within 6 minutes. The subordinate male retreated

TABLE 8
INCIDENCE OF THE MALE *WIP WIP* CALL WITH AGGRESSIVE OR SEXUAL BEHAVIOR[1]

| Situation | Number of *wip wip* calls | Per cent of total calls |
|---|---|---|
| Preceding attack on male | 110 | 37 |
| During attack on male | 66 | 22 |
| Following attack on male | 70 | 24 |
| Aggression to the female | 6 | 2 |
| During tidbitting or copulation | 36 | 12 |
| Calling by subordinate male | 3 | 1 |

[1] Twenty encounters April to June 1964.

and frequently crouched with his head in a corner. Aggression ranged from physical contact (scratching, pecking, and beating with wings) to open-mouth threat in which the red gape was conspicuously exposed. Of 201 *wip wip* calls 84 per cent were given by dominant males when fighting subordinates (Table 8); 14 per cent were associated with aggression and tidbitting to the female, but these may have been directed to the subordinate male. *Wip wip* calls indicated that attack was imminent or in progress. The close association with dominance shows aggressive motivation. *Wip wip* calls given during courtship and tidbitting reflect aggressiveness to the female, as Stokes (1963) has demonstrated in the Chukar Partridge.

*The tidbitting food call.*—A sequence of behavior performed by domestic cock chickens during courtship is tidbitting (Domm, 1927). It consists of exaggerated pecking movements directed by the male to food and other objects. The behavior has been described for several galliform species (Wood-Gush, 1954, 1956; Stokes, 1961, 1963; Kruijt, 1964; Williams et al., 1968).

Tidbitting in the California Quail consisted of pecking movements at food or the ground, usually accompanied by the low *tu tu* feeding call (Figure 2D). Meal worms, corn, and other grain not normally seen by the quail released the male call. Receptive females approached the male and both fed or intention pecked. As with the Bobwhite or Ring-necked Pheasant, the California Quail male increases the frequency of the *tu* note as the female approaches (Williams et al., 1968).

*Calls associated with copulation.*—Both sexes give specific calls before, during, and after copulation. Copulation was solicited by females after sexual deprivation by crouching with head extended. Similar crouching prior to copulation has been described for several species of galliforms (Jenkins, 1961; Stokes, 1961; Kruijt, 1964). Crouching was frequently accompanied by a thin, peeping call (Figure 8B). A receptive male on hearing this call approached the female from the rear and mounted im-

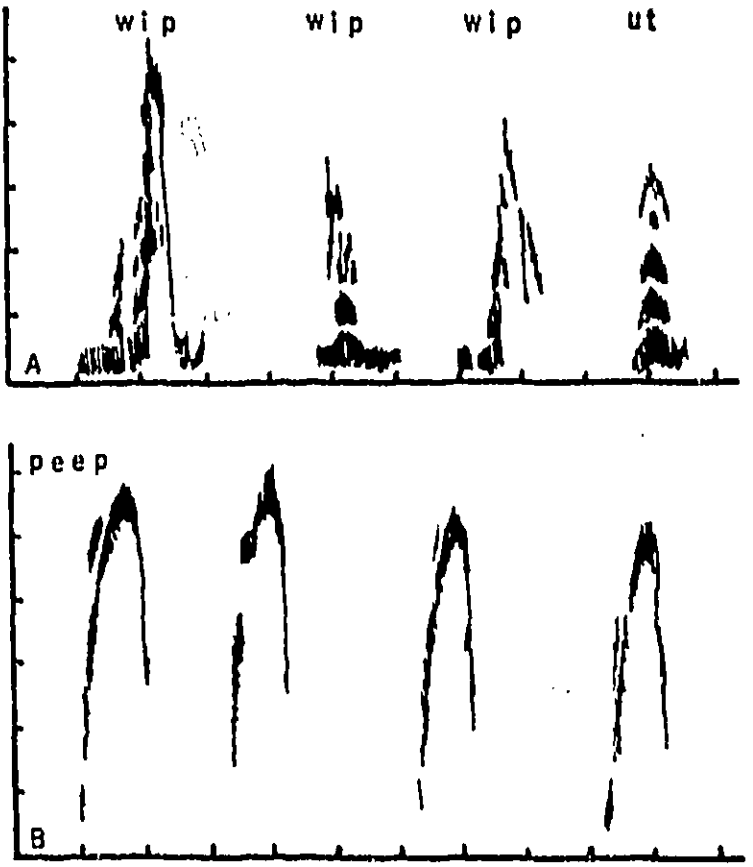


Figure 8. (A) Male and (B) female calls given during copulation. Scale as in Figure 1.

mediately without preliminary display. Some females did not call until the male mounted and grasped the base of the topknot. Other females remained quiet before and during copulation.

Males approaching a crouched female normally gave several low *ut ut* notes changing to *wip wip* note on mounting. This note continued through treading and sometimes after the male dismounted. The male gave several *ut ut* notes as the female moved away (Figure 8A). The motivation of these calls in this situation seems similar to other situations where *ut* is a contact call and *wip* an aggressive call.

Although the repetitive peeping call given by the female before and during copulation sounds like the *pseu pseu* of a bird held in the hand,

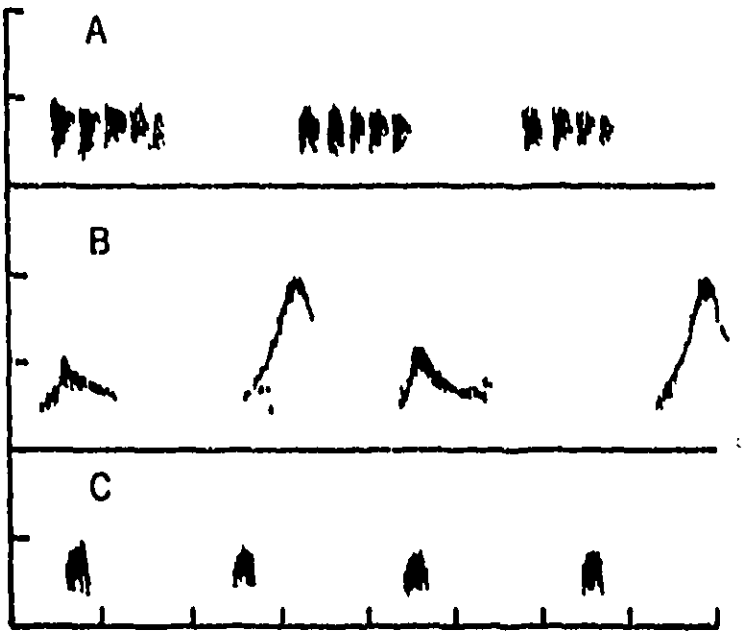


Figure 9. Calls given by male (A) and female (B) quail during nest building. (C) *Mo mo mo* call given by both sexes with chicks. Scale as in Figure 1.

these two show little similarity of form (compare Figures 3F and 8B). The copulation call of the male has a form similar to the *wip wip* heard in aggressive situations (compare Figures 8A and 7B).

*The* pa pa pa *call.*—Both males and females while building the nest uttered a low, repetitive call. In the six instances of nest building that I watched, the female selected the nest site. She made the initial scrape, after a brief period of scratching, by rotating her body while squatting on the ground. The female arranged nest material with her beak and intermittently gave a low clucking or *pa pa pa* call (Figure 9B). The male remained close to the nest site and frequently manipulated grass or other material from outside the nest. Males frequently tossed short sticks and grass over their back by flicking their head to the side and rear. They never picked up and carried materials to the nest, although they often picked up pieces tossed a few inches and threw them again. I have also seen similar behavior in the Bobwhite Quail. After a brief period on the nest the female usually left and the male entered. His behavior was similar to the female's. The call he gives during this activity is pictured in Figure 9A.

### Parental Calls

*Incubation.*—During the 22–23 days of incubation the female remains silent while on the nest. Both sexes give the *ut ut* contact note during morning and evening periods when the female leaves the nest to feed and dust. The male appears much more nervous and remains alert as the female feeds. Males do not share in incubation but remain on guard as described by Sumner (1935).

Bobwhite Quail frequently defend the nest from approach by a potential predator (Stokes, 1967). Characteristic behavior in such instances is the wing-out display with actual attacks on the predator. This is frequently followed by injury-feigning behavior accompanied by a thin, peeping call. I was unsuccessful in repeated attempts to produce this behavior in the California Quail. The female often remained on the nest until touched and then fled giving the running alarm note followed by the *pit pit* call. Both sexes gave the *pit pit* note constantly after the female left the nest.

*Brooding behavior and call.*—The female remains on the nest with the chicks from 12 to 14 hours after hatching. Both adults brood after the young leave the nest. Parent birds give a low *mo mo mo* call (Figure 9) when the chicks become slightly scattered. This call has the repetitive character of the *ut ut* call but is given more softly. No sexual differences are apparent from the sonograms.

Chicks that are completely separated from the adults give a loud *peep peep* call. This produces a low *cu ca cow* calling by one or both adults. Many times when the adults gave the *pit pit* call the brood fled to cover and remained silent and motionless. When one or both adults gave the *cu ca cow* they ran to the adults. Playback of recorded chick *peep peep* calls always produced the *cu ca cow* call from adult birds with chicks. The male called more frequently than the female. Adults without chicks frequently responded in a similar manner.

A garter snake (*Thamnophis*) placed in the pen with adults and chicks released behavior in defense of the chicks. Both male and female attacked the snake, beat it with their wings, and pecked it about the head. They gave the *pit pit* call continuously.

No specific call for gathering the chicks to be brooded was heard. Adults preparing for the night crouch on the ground and give the *cu ca cow* softly until all of the chicks are brooded. Playback of a chick *peep peep* call after the group was settled caused the male to give the *cu ca cow* call. Loud *cu ca cow* calling by the female in the parental situation frequently made the male give the sneeze call.

Although the adults did not actively feed the young, discovery of food such as a mealworm stimulated the adult food call. Chicks responded

by immediately approaching the calling adult. Quail chicks also readily responded to the similar food call of bantam hens.

*Possible additional calls not recorded.*—Sumner (1935) describes the "decoy ruse call" that he heard a female California Quail give only once during his 30-month study. The call was a "thin, peeping distress cry" given as the female with chicks "struggled and fluttered in the dust as though mortally wounded." I have noted comparable behavior in the Bobwhite Quail and Chukar Partridge, but repeated attempts to elicit it in this species were unsuccessful.

Stokes (1961) describes an "escape squeal" given by a subordinate Chukar Partridge being strongly dominated by another. I have heard this call in the Pheasant and Chicken but nothing like it from the California Quail.

Possibly both these calls exist in the species, but their infrequent use suggests they have little significance in the total behavior pattern.

## Discussion

Bird calls have evolved under the selective pressure of the environment. Crook (1964) in his analysis of weaverbirds shows that the habitat and food of the individual species within the group dictate the nature of their social and reproductive behavior, including displays and vocalizations. Ficken and Ficken (1962) show that the high-pitched calls of the wood warblers (2.6–8.9 kc/sec) are less subject to deadening by the vegetation and other barriers in their woodland habitat than are lower pitched calls. Marler (1959) found that the physical characteristics of bird calls are closely attuned to the information that they impart. In addition to their species-specific signal, bird calls may also indicate the precise location and individual identity of the calling bird. Most of the California Quail calls seem to follow these principles of adaptiveness.

The California Quail calls can be divided into four general categories based upon their physical characteristics. The first includes calls of brief duration but wide frequency range (*pit pit*, Figure 3A; *wip wip*, Figure 7B; and sneeze, Figure 7A). Calls of this nature are easy to pinpoint precisely as to source and include the mobbing calls of many birds (Marler, 1959). For *mobbing* to be effective the caller must be able to attract other birds to it and the predator. The *pit pit* call has just this function. The *wip wip* and sneeze are aggressive. If they are to function best in repelling rival males, it is equally important that they impart the precise location of the calling bird.

A second category includes calls of low, restricted amplitude, short duration, and frequent repetition. It includes the *ut ut* (Figure 2A, B, and D), *tu tu* (Figure 2D), *mo mo* (Figure 9), and calls both sexes give during nest

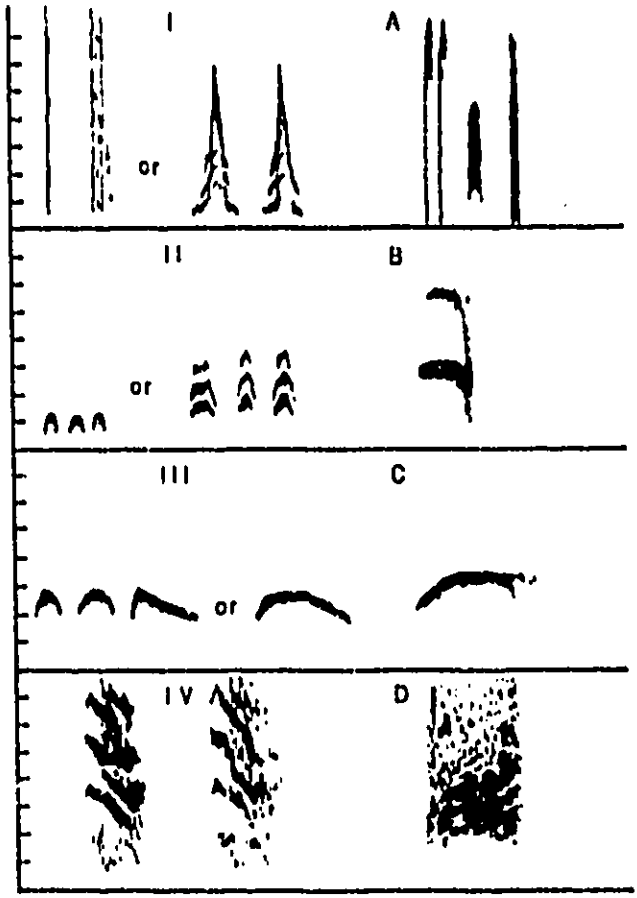


Figure 10. Comparison of call forms of California Quail (shown schematically on left) with similar calls of other birds (on the right). (A) mobbing calls of three passerines (Marler, 1957); (B) regrouping call of Bullfinch (*Pyrrhula pyrrhula*) (Bremond, 1964); (C) song of Nuthatch (*Sitta europaea*) (Bremond, 1963); (D) distress call of the Jay (*Garrulus glandarius*) (Colloque, 1960).

building (Figure 9A and B). These calls function to maintain individual contact at short distances.

The third category has restricted frequency range and extended duration. It includes the *cu ca cow* (Figure 1) and the *cow* calls (Figure 6). These two calls function to bring individuals together from long distances. The calling bird must be heard and announce its location, but not indicate it too readily to potential predators. In effect the calls appear to be a

TABLE 9

CALLS OF THE ADULT CALIFORNIA QUAIL IN RELATION TO CAUSATION AND FUNCTION

| Category | Call | Sex calling | | Causation | Functions in |
|---|---|---|---|---|---|
| Social contact | *co ca cow*[1] | M | F | separation from covey | location of covey<br>distance reduction |
| | | | | separation from mate | location of mate<br>distance reduction |
| | *ut ut*[1] | M | F | nonsexual contact | contact between individuals |
| Alarm | *pit pit*[1] | M | F | ground alarm situation | alerting-mobbing response |
| | *kurr kurr*[1] | M | F | aerial alarm situation | alarm-seeking cover |
| | *put put*[1] | M | F | continuing alarm | maintenance of alarm response |
| | *chwip chwip* | M | F | fleeing situation | alerting (?) |
| | *pow pow* | M | F | grasped by predator | alerting-mobbing response |
| Reproductive | *cow* | M | – | sexual motivation<br>unmated situation | location of unmated female |
| | *wip wip* | M | – | aggressive situation | increasing distance |
| | *sneeze* | M | – | aggressive situation<br>(thwarting?) | increasing distance |
| | *nest ceremony* | M | F | suitable nest site<br>sexual motivation | nest location (?)<br>attracting female |
| | *tu tu*[1] | M | F | presence of food<br>sexual motivation<br>presence of food | gathering at food<br>distance reduction<br>appeasement |
| | *copulation* | M | F | sexual motivation<br>copulation | inciting |
| Parental | *mo mo* | M | F | contact with chicks | contact |

[1] Calls also given in parent-young context

compromise between these various selective pressures, which affords protection from the accipitrine hawk that makes the single pass over the area and, by the call's repetition, allows a distant quail to orient successfully. The compromise is represented in the form of the call: it is intermediate between the easy-to-locate vertical configuration and the difficult-to-locate horizontal configuration (Marler, 1959).

The final category is unlike any of the above and consists of calls with broad frequency range, extended duration, and frequent repetition. The fundamental frequencies of calls of this type are generally slurred and downward-sloping and are characteristic of the severe distress calls of this and several other species (Figure 3F). Figure 10 shows a generalized form of these call categories in comparison to similar calls of several other species.

Table 9 summarizes the calls of the California Quail within four functional categories. Gregariousness and reproduction are facilitated by three calls given in five situations of individual contact between birds of a nonbreeding group or pair. Five of the vocalizations are associated with alarm, three conveying precise information as to the type of alarm and releasing specific responses suited for avoidance. That only two of the calls are agonistic indicates a relative compatibility even during reproduction.

TABLE 10

Comparison of General Call Types of Gregarious (G) and More Solitary (S) Species

| Context in which given | Species and habit | | | | | | |
|---|---|---|---|---|---|---|---|
| | Calif. Quail G | Bob Quail[1] G | Dom. fowl Junglefowl[2] G | Chuck. Part.[3] G | Chaffinch[4] S | Afr. Vill.[5] Weav. S | Blackbird[6] S |
| Flight | . | + | . | + | + | + | + |
| Gathering | + | + | . | + | . | . | . |
| Group contact | + | + | . | + | + | . | + |
| Group feeding | + | + | . | + | ? | . | . |
| Roosting | . | + | . | . | . | . | + |
| General alarm | . | . | + | . | + | . | + |
| Flying predator | + | + | + | + | + | | + |
| Ground predator | + | + | + | + | + | . | + |
| Continuing alarm | + | . | . | . | + | . | . |
| Fleeing alarm | + | + | . | . | + | . | . |
| Hand-held alarm | + | + | + | + | + | . | + |
| Territorial | . | + | + | + | | + | + |
| Group territorial | . | + | . | + | . | | . |
| Aggressive | + | + | + | + | + | +(3) | . |
| Courtship | . | . | | . | +(3) | + | + |
| Mate feeding | + | + | + | + | . | . | . |
| Nest building | + | + | + | + | . | + | . |
| Copulation | + | + | + | + | + | + | . |
| Total call types listed | 12 | 15 | 9 | 13 | 11 | 8 | 9 |

[1] Stokes, 1967. [2] Konishi, 1964. [3] Stokes, 1964. [4] Marler, 1956. [5] Collias, 1964. [6] Messmer and Messmer 1936, Snow, 1958.

Table 10 compares the types of calls of four gregarious *galliforms* with three of more solitary passerines. Although the repertoire of California Quail calls is essentially the same as for the Bobwhite Quail and Chukar Partridge, several differences are apparent. The rally call of the Chukar serves to regroup separated individuals. In this situation it is comparable to the *cu ca cow* of the California Quail. During reproduction Chukars, unlike male quail, continue to call after pairing. Both the rally call and the *cu ca cow* serve to bring the sexes together for mating, but the rally call continues to function in agonistic situations to space the males and hence is like typical bird song (Williams and Stokes, 1965). The same is true for the crow of the polygamous Junglefowl and the Ring-necked Pheasant. Males of these species do not share in the care of young and also lack the parental calls given by the male quail of the California species.

During the nonbreeding season the *koi-lee* call of the Bobwhite (Stokes, 1967) and the rally call of the Chukar (Williams and Stokes, 1965) keep coveys apprised of the location of other coveys, possibly with epideictic function (Wynne-Edwards, 1962) of regulating density. No such call exists in the California Quail. Stoddard (1931) shows a mean winter covey size of 14 birds for the Bobwhite, whereas McLean (in Gorsuch,

1934, p. 17) reports 2,000 California Quail in a single winter flock and Sumner (1935) records a mean of 35 birds in winter coveys. The latter covey size indicates that three to five family groups have united, whereas Bobwhite covey size reflects only one or two family groups. If all the *California Quail coveys within a limited area come together for the winter,* no call to space coveys is necessary.

A possible explanation for the differences in covey size between the Bobwhite Quail and both the California and Gambel Quail may be the *differences of habitat and food availability. Gorsuch (1934) shows a* close correlation between appearance of "winter annuals" and amalgamation of coveys of Gambel Quail into large winter flocks. He points out that this habit is not so much a strong tendency to associate with other birds, as a coming together in a restricted area containing suitable food or water. The same is probably true for the California Quail, particularly in the more arid parts of its range and where much of its range is subject to periodic brush fires. The habitat of the southeastern United States, which is typical for the Bobwhite, offers a more evenly distributed and constant source of winter food so that this species is not forced into large concentrations.

The gathering and group-feeding calls are lacking in less gregarious species such as the Chaffinch (*Fringilla coelebs*) and Blackbird (*Turdus merula*). Flight calls seem to serve in the same manner as the short-range contact call of the gregarious species. Collias (1963) shows that 7 of the 15 vocalizations of the African Village Weaverbird (*Textor cucullatus*) are associated with their complex mating and nesting habits. The comparatively simple courtship and nesting of California Quail is accompanied by only three vocalizations.

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## Summary

The calls of captive California Quail (*Lophortyx californicus*) were studied from June 1961 to August 1964. By means of the audiospectrograph 14 adult call types are described and analyzed. Each call is related to causation and function. Causation includes the environmental and social situation plus the internal motivation to call. Immediate function was

measured by the effect of the call on the behavior of other birds of the same species. Long-term function or adaptiveness of each call is considered in relation to the habitat and habit of the species. Calling in this species is compared with that in other birds of the same and more solitary habits.

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